SHORTER ARTICLES AND DISCUSSIONS

THE TORTOISESHELL CAT

In *The Journal of Genetics* (June, 1913), Doncaster has summarized genetic data dealing with the tortoiseshell cat. The records are collected from fancy breeders and from the work of Dr. C. C. Little.

Aside from certain disputed points the inheritance is in accordance with simple sex-linkage and is analogous to the human defects—color-blindness, night-blindness, nystagmus, and hemophilia, and to the thirty or more sex-linked factors of *Drosophila*.

If the factor for yellow be represented by Y and its allelomorph, the factor for black, by B, the lack of either by b, the sex factor by X, and the allelomorph of X by x, the normal zygotic possibilities are as follows: YX — bx = yellow male. BX — bx = black male. YX — YX = yellow female. BX — BX = black female. YX — BX = tortoiseshell female.

It is obvious then that there can be but two classes of males, while there are three classes of females. Difficulties arise when it is attempted to explain the occurrence of black females produced either by the mating of a black female to a yellow male which should give only tortoiseshell females and black males. or by the mating of a tortoiseshell female to a yellow male, which should give only tortoiseshell and yellow females and black and yellow males. The occurrence of the rare tortoiseshell male is also the cause of considerable difficulty. In one mating out of seventeen of yellow females to yellow males there were produced three tortoiseshell females. There are recorded in addition from the seventeen matings forty yellow females and forty-eight yellow males which are in agreement with expectation.

In order to explain these discrepancies it is suggested that possibly the linkage of Y with X is not absolute. Yellow males may then produce gametes bX and Yx in addition to the normal or more frequent gametes YX and bx. Gamete bX is female determining, while gamete Yx is male determining and yellow bearing. The latter gamete should produce a tortoiseshell male when it meets an egg BX.

On this hypothesis we should expect the tortoiseshell males to be as frequent as the anomalous black females from yellow fathers. From the matings recorded there are eighteen anomalous black females and only three tortoiseshell males, and one of these tortoiseshell males had a black father. There is a fur-

ther objection to this hypothesis inasmuch as it is not explained how gamete bX differs from BX. Doncaster admits these difficulties, stating that further work is necessary before a definite conclusion can be reached.

In a more recent paper[1] Doncaster has suggested non-disjunction of the sex-chromosomes in oogenesis as a possible explanation. This explains the matroclinous black females, but fails to account for the lack of an equal number of patroclinous yellow males. It also fails to account for the tortoiseshell male and the occurrence of tortoiseshell females among the offspring of yellow by yellow.

In a series of experiments begun upon cats at the University of Pennsylvania during the last year, the tortoiseshell problem has been especially investigated. A yellow Persian male was crossed with common cats—black, maltese and tabby. The results, although not at present extensive, are sufficient to explain, at least in part, the anomalies observed, and to suggest a simple explanation for the occurrence of unexpected classes.

When the yellow male was crossed with a maltese female, a maltese male and two blue and cream females were produced. The blue and cream is the maltese or dilute tortoiseshell. When mated to a black female the yellow male produced both dark and dilute kittens. This shows that the black female was heterozygous for dilution. Two of the males were black and two maltese. The two females were dark tortoiseshell. When the yellow male was crossed with a dark tabby, there were produced dark and light tabbies and maltese. Blacks are also to be expected from this mating. The mother is evidently hybrid between tabby and black and between black and maltese. The female offspring showed yellow: the male offspring were without yellow except for tabby striping.

The female offspring obtained from these matings may be arranged in a series, ranging from one that is predominantly yellow to one that is maltese except for a few cream-colored hairs. The maltese with a few cream hairs occurred in the litter of three above mentioned, which included also a maltese male and a maltese female with a small cream patch.

It may be readily understood how a maltese cat with a few cream hairs or its intense form, a black cat with a few yellow hairs, would be recorded as maltese or black, and it is reasonable to suppose that further segregation of distribution factors in the direction of black would have produced a fully black female. This may

[1] *Quarterly Journal of Microscopical Science,* February, 1914.

be compared with conditions in the guinea-pig in which yellow spotting is continuous with total black. The essential differences are that in the cat we have a factor for yellow allelomorphic to a factor for black, that these allelomorphs are sex-linked, and that either alone is sufficient to produce its expected color, but that when one is balanced against the other, as in the tortoiseshell female, other factors governing the relative amounts of the two colors can act and produce continuous variation from yellow to black.

The three tortoiseshell females from the mating of yellow by yellow may be explained by supposing that the mother was gametically a tortoiseshell plus a sum of yellow extension factors and minus a sum of black extension factors.

The occurrence of the tabby factor brings in a restriction of the black pigmentation producing yellow stripes. It is therefore much more difficult to distinguish a tabby from a tabby-tortoiseshell than a black from a tortoiseshell. We have had a few tabby-tortoiseshells that would have been recorded as tabbies if close examination had not been made.

Another source of error in records involving the tortoiseshell pattern may be introduced by the occurrence of white spots. Doncaster makes no mention of these in his paper, so that it is possible that they did not occur in the animals recorded. In what is genetically a tortoiseshell and white cat the incidence of the white spotting may happen to be at just those points which would otherwise be yellow. Thus the occurrence of black and white daughters from yellow males may be explained. It is possible also that the yellow mother of the three tortoiseshell kittens recorded from the mating of yellow by yellow may have been white at points which, if pigmented, would have been black. She would then have been genetically a tortoiseshell and white and some tortoiseshell kittens would have been expected.

I would suggest as a plausible hypothesis that the rare tortoiseshell male is genetically a yellow with an extreme of black extension factors or a black with an extreme of yellow extension factors. This hypothesis is rendered more probable by some slight evidence showing that male tortoiseshells breed like yellows.

There is then no need for assuming in the cat either breaks in sex-linkage or non-disjunction of the sex chromosomes in oogenesis.

PHINEAS W. WHITING
UNIVERSITY OF PENNSYLVANIA